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EVIDENCE FOR *MACROTUS CALIFORNICUS* FROM TERLINGUA, TEXAS

CLAYTON E. RAY AND DON E. WILSON

In a footnote to the description of a fossil land snail, Cockerell (1930) mentioned associated bones of *Equus*, *Bison*, and *Ovis*, and "a quantity of Bat remains . . . in which Dr. Gerrit S. Miller recognizes *Macrotus californicus* and a race somewhat larger than *Desmodus rotundus murinus*." The specimens were said to have been recovered from a limestone crevice-filling 350 feet (170 meters) down in a cinnabar mine near Terlingua, Brewster County, in the Big Bend region of western Texas. Although the chiropteran records have been noted subsequently (Anderson, 1969, *Macrotus* only; Martin, 1972; Schmidly, 1977; Smith, 1976), the evidence has never been documented properly. Recently the Denver Museum of Natural History (DMNH) loaned the chiropteran material to C. E. Ray in connection with a review of fossil vampire bats (Ray and Linares, in press). Having available the fossils and detailed modern taxonomic studies of *Macrotus* (Anderson and Nelson, 1965; Buden, 1975; Davis and Baker, 1974; Greenbaum and Baker, 1976) makes it feasible, timely, and potentially significant to evaluate and present the evidence for *Macrotus*. This is the only fossil record for the mainland, and it lies in a geographically interesting position approximately 450 kilometers from the closest modern records, in southwestern Chihuahua (Anderson, 1972).

Ray and Linares (in press) have reviewed what is known of the Terlingua record, primarily from correspondence between Gerrit S. Miller and Harold J. Cook of the Colorado (now Denver)

Museum of Natural History, and from Lonsdale (1929). They determined that the fossils came from the Little Thirty-Eight Mine, approximately 2.5 miles west of the present location of Terlingua (29°19'20" N, 103°36'45" W). Lonsdale (1929) described "a small gallery some three feet in diameter" at a depth of 320 (not 350) feet. This chamber, incompletely filled by clay with mud cracks on its surface, is the probable source of the fossils. Yates and Thompson (1959) provided a detailed account of the mine and its history. Unfortunately, there is no way to determine the precise geologic age of the bat remains, but their amber to brown color, glassy permineralization, and association with extinct taxa recommend tentative assignment of a late Pleistocene (Rancholabrean) age. There is nothing in the occurrence indicative of Recent origin.

In addition to *Desmodus*, Miller (letter to Cook of 4 June 1929) identified "a *Macrotus* . . . very close to *M. californicus*" and stated, "It will be all right to record [the genus] if you wish, but I should not care to be quoted as authority for anything more—that is, without at least . . . several skulls of the *Macrotus* I do not care to attempt specific determination." In a subsequent letter (19 February 1930) he remarked, "I can see nothing to distinguish the *Macrotus* from *M. californicus*." The specimens on which these statements were based, still in the vials with Miller's labels apparently just as he returned them to the Colorado Museum of Natural History on 21 February 1930, include the following: 1) Lot no. 1161, distal half of left and distal two-thirds and proximal end of right humerus; two left, one right, and several fragments of radii; several fragments of metacarpals; one distal half and two proximal ends of left femora; one right tibia; and 2) Lot no. 1168, partial skull (Fig. 1) with second premolars and all molars, but lacking tip of rostrum, most of braincase and basicranium, and most of zygomata; four left and five right humeri (one of each lacking head); four left, four right, and six partial radii; one right tibia. Not surprisingly, Miller's identifications were correct; additional fragments, wisely left unidentified by Miller, very likely also pertain to *Macrotus*. Besides being the mark of a careful taxonomist, Miller's reticence at specific determination is understandable in that four species of *Macrotus* were then recognized, and the genus had not yet been the subject of the thorough analyses now available. We accept the recognition of two species, *M. californicus* and *M. waterhousii*, following Davis and Baker (1974), and reinforced by Greenbaum and Baker (1976).

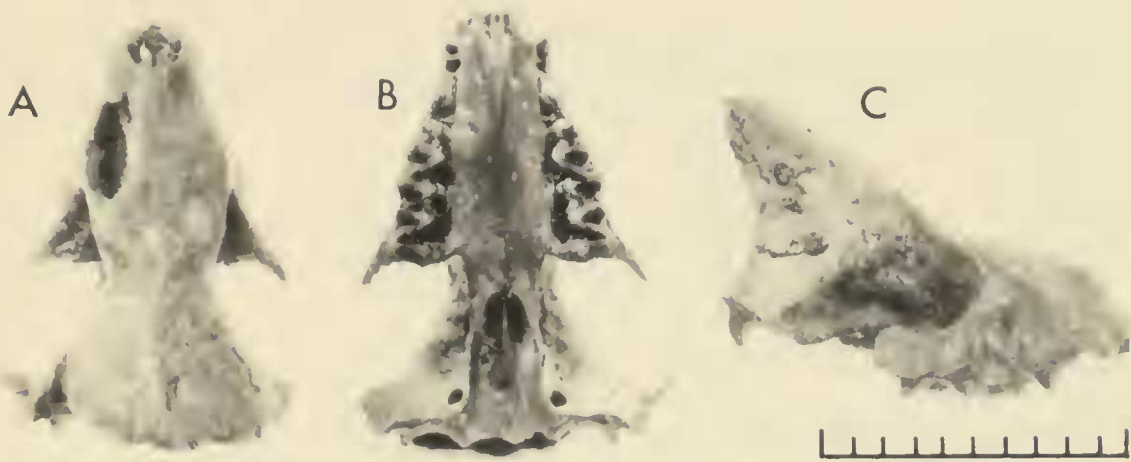


FIG. 1.—Partial skull of *Macrotus californicus* from Little Thirty-Eight cinnabar mine, near Terlingua, Texas, DMNH Lot no. 1168, in dorsal (A), ventral (B), and lateral (C) aspects. Scale is in millimeters.

Of the measurements used in recent taxonomic studies of *Macrotus*, we were able to make the following (recorded in millimeters) on the partial skull: interorbital breadth, 3.5; posterior zygomatic breadth, 8.8; maxillary toothrow (right), 8.1; maxillary toothrow (right), 8.1; width at M^2 , 7.2; canine breadth, 3.5; length of second upper premolar, 1.7. These dimensions place the fossil within the observed size range of modern *Macrotus* (Anderson and Nelson, 1965; Buden, 1975; our Table 1), but specific assignment is less certain. Davis and Baker (1974:34) stated that "an interorbital breadth of 3.8 mm or less is indicative of *M. californicus*, 3.8 mm or more being *M. waterhousii*." Although we have found some overlap in interorbital breadth (see Davis and Baker, 1974), the value of 3.5 mm. for the fossil supports assignment to *M. californicus*.

In an attempt to identify the Terlingua specimen, we applied a stepwise Discriminant Function Analysis (BMD-07M, Dixon, 1973) to the first five measurable characters listed above for the fossil and to three groups of Recent comparative material: *M. californicus* ($N=210$), *M. w. bulleri* ($N=147$), and *M. w. mexicanus* ($N=33$). Basically, this technique allocates unknown specimens to one of two or more previously defined groups (Sokal and Rohlf, 1969; Sneath and Sokal, 1973; Wilson, 1973; and Nie *et al.*, 1975). It computes new canonical variables that are linear functions of the standardized original variables, thus maximizing separation between the groups. Then, unknown specimens are scored on the same canonical variables and allocated to the group to which they are phenetically closest.

The Terlingua specimen is intermediate between *M. californicus* and *M. w. bulleri* on the first canonical variable and below

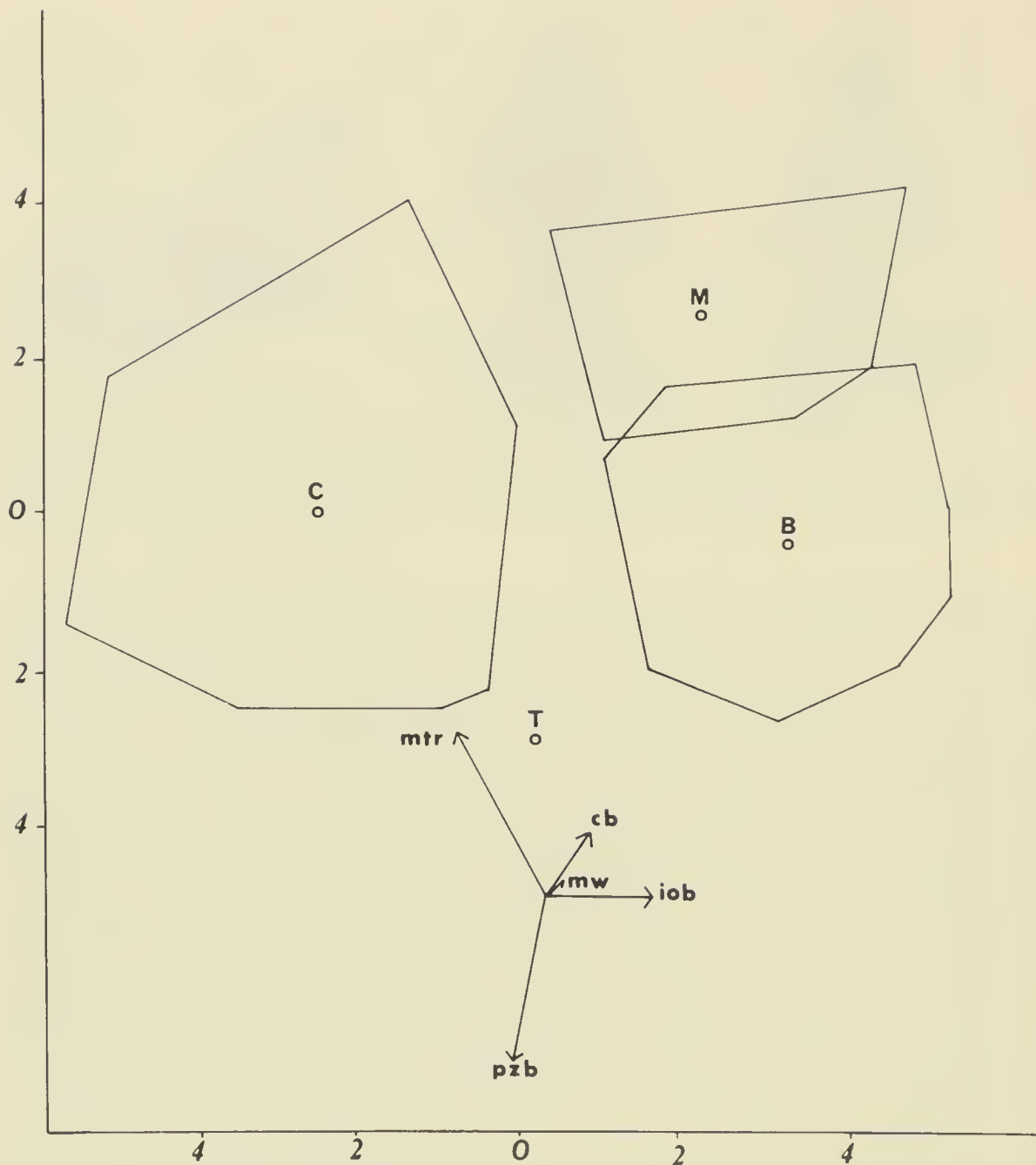


FIG. 2.—Plot of the first (abscissa) and second (ordinate) canonical variables. Arrows show direction of canonical character vectors and lengths of lines indicate relative contribution of original characters in canonical analysis. Abbreviations are as follows: C, *Macrotus californicus*; M, *Macrotus waterhousii mexicanus*; B, *Macrotus waterhousii bulleri*; T, Terlingua fossil; mtr, maxillary toothrow length; cb, canine breadth; mw, width across M²; iob, interorbital breadth; pzb, posterior zygomatic breadth.

the range of both species on the second (Fig. 2). The probability that the specimen belongs with *M. californicus* is 0.516 and that it belongs with *M. w. bulleri* is 0.484. The positions of the reference groups and the fossil specimen are shown on the first two canonical variates in Fig. 2.

The intermediacy demonstrated by the discriminant function analysis is somewhat surprising but may be more understandable

TABLE 1.—Means and standard deviations of groups used in the Discriminant Function Analysis, and from the literature records of Anderson and Nelson, 1965 (Tamaulipas) and Alvarez and Ramírez-Pulido, 1972 (San Luis Potosí).

Specimens	Interorbital breadth	Posterior zygomatic breadth	Maxillary toothrow length	Width at M ²	Canine breadth
<i>Macrotus californicus</i> (N=210)	3.5±0.12	8.8±0.28	8.9±0.20	7.3±0.19	3.2±0.14
<i>M. waterhousi bulleri</i> (N=117)	1.0±0.10	9.0±0.19	8.6±0.18	7.1±0.16	3.6±0.13
<i>M. w. mexicanus</i> (N=33)	1.0±0.12	9.2±0.23	9.2±0.16	7.7±0.18	3.8±0.14
Terlingua fossil	3.5	8.8	8.1	7.2	3.5
Tamaulipas (N=1)	3.6±0.08				3.5±0.10
San Luis Potosí (N=11)	3.6				3.5

upon a closer examination of the data set. Given the overall morphological similarity of the two species, the use of a small set of obviously size-correlated characters is less than ideal for a definitive classification using a multivariate technique. In spite of the equivocal results of this analysis, we are willing to assign the specimen to *M. californicus*, relying principally upon the previously demonstrated usefulness of interorbital breadth as the most critical measurement in our data set. Perhaps this is a case in which modern taxonomic tools need to be tempered with more classical systematic judgment.

Table 1 presents means and standard deviations for all specimens used in the analysis. The fossil specimen is closer to *M. californicus* in all measurements except canine breadth. The relatively short maxillary toothrow reported for the fossil may reflect in part the loss of its canines and the fact that the measurement was taken under a microscope. The reference material was measured with dial calipers, and most specimens had the canines in place, which may have resulted in lengths slightly longer than alveolar. However, the difference, if any, is slight, and we are convinced that the fossil does in fact have a shorter toothrow than the average Recent specimen.

The Terlingua specimen appears to represent *M. californicus*, but without comparative material of the same geologic age, an assessment of variation is impossible. We suggest that the difference between the Terlingua specimen and Recent *M. californicus*

is a reflection of minor phenetic change that has occurred within the species since Rancholabrean time. Such change is to be expected in a species whose distribution spans a geographic area that has undergone periodic climatic and environmental shifts over the past 10,000 to 15,000 years. We would argue further that, although documentation of such change is of interest to evolutionary biologists, taxonomic recognition of these minor variations is unwarranted.

The fossil postcranial material is readily referable to *Macrotus* on the basis of size and form (see Vaughan, 1959, for detailed description and illustration of the major skeletal elements of *M. californicus*), but specific characters were not found in the modern skeletons available in the National Museum of Natural History (three adult *M. californicus*, six *M. waterhousii*). Total lengths were measured on one humerus, radius, and tibia of each modern specimen, and on the available seven humeri, 11 radii, and two tibiae among the fossils. No patterns of variation emerged other than a slight suggestion of larger average size among the fossils. This would be worth investigating when larger samples are available of both fossil and modern *Macrotus*.

Anderson and Nelson (1965) examined 10 specimens from Jaumave (23°25'N, 99°23'W), Tamaulipas, which they recognized as widely disjunct representatives of *M. californicus* (regarded by them as a subspecies of *M. waterhousii*), and pointed out the absence of *Macrotus* from the plateau of northcentral México. Villa-R. (1967) rejected Anderson and Nelson's (1965) interpretation, in part on the mistaken impression that the specimens from Jaumave were subfossils, and excluded the record from the distribution of *Macrotus*. Also, without presenting supportive evidence, he mapped the distribution of *M. waterhousii bulleri* as blanketing much of the plateau of northcentral México, with northern marginal records in Sonora and western Chihuahua on the west and in Nuevo León on the east (one individual from Cueva de Guadalupe, Quebrada de Iturbide, 24°44'N, 99°54'W). Choate and Clifton (1970), following Anderson and Nelson (1965), assigned to *M. w. californicus* a single specimen from a second locality in Tamaulipas very close to Jaumave ("Conrado Castillo," 19 miles SW Ciudad Victoria).

Jones *et al.* (1977), apparently on the basis of Villa-R. (1967), indicated the distribution of *M. californicus* as "northwestern México (Baja California, Chihuahua, Sonora, and northern Sinaloa) northward into the United States" and that of *M. water-*

housii as "western (Sonora) and eastern (Tamaulipas) México southward to the Yucatán Peninsula and Guatemala." They did not mention the important findings of Alvarez and Ramírez-Pulido (1972) on *Macrotus*, although this work was cited. Alvarez and Ramírez-Pulido (1972) noted and explained the source of confusion regarding the sample from Jaumave, found the assignment of the single specimen reported by Villa-R. (1967) from Nuevo León to be equivocal, and (of greatest significance) added a sample of 11 specimens from 2 kilometers west of El Custodio (22°39'N, 99°58'W), San Luis Potosí. They assigned the material to *M. w. californicus*, now *M. californicus* (see Table 1), which greatly expands the probable distribution of the species in northeastern México.

Figure 1 of Alvarez and Ramírez-Pulido (1972) incorporates several errors that, although in no way altering the correctness of their conclusions, collectively obscure their basis. The purpose of the figure is to show the position of the sample from El Custodio in relation to samples of *M. californicus* and *M. waterhousii* measured by Anderson and Nelson (1965). Samples D and E represent *M. californicus*, not *M. w. bulleri*, and interorbital breadth for sample D is misplotted, possibly as a result of transposing digits, with the mean shown (incorrectly) as 3.75 rather than 3.57. Sample F in the figure is actually the sample from El Custodio, and the unlabeled sample in the figure is actually sample F. The true sample F and samples G-I are *M. waterhousii*. The dashed line separating *bulleri* and *californicus* in the figure is placed at the correct level, with samples D, E, and El Custodio above, and F-I below. The label *californicus* should be above the line and *bulleri* below, and in fact only samples F and G represent *M. w. bulleri*, whereas H and I are *M. w. mexicanus*.

Villa-R. (1967) was concerned about the problem of explaining the seemingly anomalous disjunct distribution proposed by Anderson and Nelson (1965). Unaware at that time of the corroborative evidence from Terlingua (Anderson, personal communication), Anderson and Nelson (1965) proposed the remarkably prescient hypothesis "that during some warmer and drier period *Macrotus* [*californicus*] was distributed across the continent in the region of the present international boundary, that changing conditions have removed it from this area, and that the Tamaulipan population is a relict one." Greenbaum and Baker (1976) and Jones *et al.* (1977) either did not consider Anderson and Nelson's interpretation, strengthened by Alvarez and Ramírez-Pulido

(1972), or dismissed it without comment. Subsequent attempts to secure specimens of the eastern population of *Macrotus californicus* by R. J. Baker and colleagues were unsuccessful (R. J. Baker, personal communication). Northeastern Mexican *Macrotus* would be ideal for a further application of chromosomal and electrophoretic techniques, and an independent test of Anderson and Nelson's (1965) morphometrically and paleontologically supported hypothesis. *Macrotus* offers an extraordinary if not unique opportunity for future investigation of the questions of parapatry, introgression, dispersal, and mode(s) of speciation posed by Davis and Baker (1974) because of the essentially independent tests for the same species afforded by the eastern populations of *M. californicus* and *M. waterhousii*, which also are more meaningfully situated for comparisons with Caribbean insular populations.

Macrotus californicus is the only year around resident phyllostomatid in the United States. It does not hibernate, and, although some limited migratory movement in winter from the northernmost part (Arizona) of its range has been suggested (Anderson, 1969), this is not as yet strongly reflected in seasonal collecting data (Hoffmeister, 1970). *M. californicus* does, however, reduce its activity in winter, and seems to be sensitive to temperature and humidity and to select roosts in part on that basis (Davis, 1970; Leitner and Ray, 1964). It characteristically roosts in relatively open, large chambers, near entrances, and does not require total darkness (Anderson, 1969). The species readily enters small openings (Vaughan, 1959). In the Yuma Mine in Arizona it has been observed to be active inside during cooler weather, but not to appear outside, and to descend to greater depths, at least 61 meters, apparently in response to humid weather (Dice and Blossom, 1937). These habits are compatible with its occurrence as a well-preserved, probably not redeposited, Pleistocene fossil at a depth of 320 to 350 feet in the cave system near Terlingua.

Macrotus roosts with other bats, including *Desmodus* (Jones *et al.*, 1972; Loomis and Davis, 1965; Lukens and Davis, 1957; Villar., 1967; Watkins *et al.*, 1972), and the two have been found in association as fossils at one other locality, Cueva Centenario de Lenin in Cuba (Wołoszyn and Mayo, 1974).

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Addresses of authors: CLAYTON E. RAY, *Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560*; DON E. WILSON, *U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, National Museum of Natural History, Washington, D.C. 20560*.
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